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Feeding selectivity of sesarmid crabs from northern Australian mangrove forests

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ABSTRACT

Sesarmid crabs are possibly one of the most important components of mangrove fauna because of their influence on nutrient cycling and forest structure by feeding on litterfall. Little is known about the influence of electivity on the role of crabs in mangrove forests, and how this is affected by the availability of litter items. This study investigated electivity of three northern Australian sesarmid crabs (*Perisesarma semperi*, *Perisesarma darwinensis* and *Neosarmatium meinerti*) from leaves of various conditions and from common species, as well as the effect of the availability of propagules on feeding electivity. In almost every experiment, decayed and senescent leaves were selected over fresh leaves, and typically decayed leaves were selected over senescent. Electivity for mangrove species, however, varied among crab species and depended upon availability of litter type to select from. In experiments that included propagules as well as leaves, leaves were selected over propagules. These results suggest that the sesarmid crab species included in this study may have a greater role in nutrient cycling than in forest structuring because of their selectivity of leaves over propagules.

KEYWORDS: sesarmid, Sesarmidae, feeding behaviour, selectivity, mangrove leaves, consumption.

INTRODUCTION

Sesarmid crabs are one of the most common and abundant faunal groups in mangrove forests (Golley *et al.* 1962; Jones 1984; Smith *et al.* 1991). Recent research indicates that they play important roles in the ecology of these ecosystems (Lee 1998) and may occupy a keystone position in Australian mangrove forests (Smith *et al.* 1991). For example, crabs may affect forest structure by attacking mangrove propagules (Smith 1987; McGuinness 1997), influence nutrient cycling by feeding on litterfall (Robertson 1986), alter the properties of the soil by their burrowing activities (Smith *et al.* 1991) and be involved in competitive interactions with other species (Fratini *et al.* 2000).

Studies on the feeding ecology of sesarmid crabs have contributed to our understanding of the fate of mangrove litter nutrients (Camilleri 1984, 1989). These studies have shown that sesarmid crabs have an important role in retaining nutrients within mangrove forests and reducing export to nearby coastal systems (Lee 1997, 1998). Crabs process a variety of food items, mainly dead leaves, into smaller particles, and in this way make these nutrients more readily available for other fauna to consume (e.g. gastropods, crabs and other crustaceans). If sesarmid crabs display selectivity for particular food items, such as leaves and propagules from certain species of mangroves, this is likely to affect the quantity, type and nutritional value of mangrove litter that is recycled.

The feeding behaviour of some sesarmid crabs, in particular those common to mangrove forests in north-eastern Australia and Kenya, has been studied (Camilleri 1989; Micheli 1993; Dahdouh-Guebas *et al.* 1997; Kathiresan and Bingham 2001; Cannicci *et al.* 2007), but the range of species and locations studied, is still limited. Furthermore, previous studies did not test the effect of the availability of litter on feeding electivity. The availability of material may depend on factors such as mangrove assemblage and season. In mangrove forests in tropical Australia, for instance, most propagules drop during the wet season (Ball and Pidsley 1988) and are, therefore, only available at this time.

This study investigates feeding electivity of three species of sesarmid crabs from common mangrove species occurring in tropical mangrove forests in northern Australia, and how electivity is affected by the seasonal availability of propagules. The specific aim is to examine electivity of mangrove leaves from three different species and three conditions during wet and dry season conditions (with and without the presence of propagules). Finally, other variables which might affect consumption – crab size (see Emmerson and McGwynne 1992) and sex (see Olafsson *et al.* 2002) – were also investigated.

MATERIALS AND METHODS

Crabs. The three most abundant sesarmid crabs in the dominant mangrove assemblages in Darwin Harbour (Salgado Kent 2004) were studied: *Perisesarma semperi*, *P. darwinensis*, and *Neosarmatium meinerti*. *Neosarmatium meinerti* is most abundant in mid to upper shore mixed woodland and hinterland assemblages (Salgado Kent 2004) dominated by *Ceriops australis* and *Avicennia marina* (naming of assemblages follows Brocklehurst and Edmeades 1996). *Perisesarma darwinensis* is common in tidal flat assemblages dominated by *C. australis*, but *P. semperi* is found in tidal bank assemblages dominated by *A. marina* and *Rhizophora stylosa* (Salgado Kent 2004; pers. obs.). All crabs were collected from the forest at Jones Creek, Darwin Harbour. Twenty individuals – ten of each sex – of the two *Perisesarma* species were collected by hand: half the crabs were larger, and half smaller, than the average size (1.3 cm in carapace width). Average size did not differ between species and was estimated from 106 crabs that were collected and measured prior to these experiments. *Neosarmatium meinerti* crabs were captured in funneled pitfall traps (similar to the pitfall traps used by Warren (1987)). Results for *N. meinerti* did not include analyses on sex and size because only six individuals could be captured, only one of which was female. All crabs were placed in separate containers as soon as possible upon return to the laboratory, to reduce stress and injury, in particular among aggressive competing males.

Leaf preparation. The leaves and propagules used in the experiments were taken from the three dominant mangrove species in the four assemblages inhabited by the crabs: *A. marina*, *C. australis* and *R. stylosa*. Leaf conditions included fresh (green leaves), senescent (yellow leaves) and decayed (brown leaves). Fresh and senescent leaves were collected directly from trees. Fresh leaves can frequently occur on the forest floor when storms, which are common in the wet season, knock them down. Decayed leaves were prepared by collecting senescent leaves from trees and leaving these to decompose for fifteen days, enclosed in 2 mm mesh bags tied to mangrove roots (as in Robertson (1988)). All leaves were stored at 4°C for 1 to 1.5 days, until the experiments began. Circular sections of leaf, 2 cm in diameter, were used in experiments here to reduce possible influences of leaf size on electivity (as in Camilleri 1989). Propagules were collected from trees and were also cut into similar sized pieces (to each other and to the leaves).

Experiment preparation. All experiments were conducted in a shaded, outdoor laboratory in which crabs experienced a regular diurnal cycle, and conditions similar to those prevailing in the field at that season. Crabs were placed individually into clear, plastic containers, 14 cm in diameter and 10 cm high. A circle 6 cm in diameter in the centre of each container's lid was cut out and this allowed air to enter but prevented the crabs from escaping. Containers without crabs were included in experiments to control for weight changes due to leaching of dissolved organic matter (DOM) and fungal and microbial activity. Seawater was added to all containers to a level of 0.5 cm and was changed daily (to ensure that lack of moisture was not a factor affecting results, since the crabs inhabit waterlogged environments). Most habitats where these crabs were prevalent were saturated with water (with the exception of *N. meinerti*). Crabs were starved for 24 hours before each experiment. During the experiments, *Perisesarma* crabs were offered a choice of mangrove material for a period of 12 hours. In each experiment, the amount offered was one disc or piece for each type x species (and each species x condition, for leaves) to be included for testing. The amount of material offered was great enough to allow for detection of significant patterns in electivity, but small enough so that sufficient quantities of material from discs and/or pieces remained to retain information on patterns in electivity. For this reason *N. meinerti* crabs were offered mangrove material for a period of 18 hours, as these crabs took longer to consume a significant amount of material. The material offered to crabs was randomly placed within the containers. Each batch of crabs was used in no more than two experiments to ensure that their condition did not deteriorate significantly and affect the results of the experiments.

Experiments. Two experiments were conducted (Table 1). The first included leaves from all three mangrove species and three leaf conditions, and the second included the addition of propagules from all three mangrove species. In mangrove forests of Darwin Harbour, Northern Territory, the dominance of different mangroves species differs among habitats where *N. meinerti*, *P. semperi* and *P. darwinensis* are most abundant. However, all three mangrove species overlap in distribution with the three crab species to various extents (Brocklehurst and Edmeades 1996). Hence, in the natural environment, the chance of encounter of leaves and propagules of these mangrove species by the three species is realistic, and in most cases relatively high.

To test for seasonal differences, experiments were done under wet and dry season conditions (outdoor laboratory experiments ensured that crabs experienced seasonal changes in humidity and temperature). Dry season experiments used only leaves but wet season experiments used both propagules and leaves. A pilot study found no significant effect of propagule dimension on feeding electivity (Salgado Kent 2004). Each experiment described below simultaneously examined feeding electivity of the different species of crabs. 'Dry Season' experiments were done simultaneously (and in the dry season), and 'Wet Season' experiments were done simultaneously (in the wet season).

Table 1. Material included in experiments testing electivity of sesarmid crabs for mangrove leaves and propagules. The mangrove species were Am = *Avicennia marina*; Ca = *Ceriops australis*; Rs = *Rhizophora stylosa*. The sesarmid crabs were Ps = *Perisesarma semperi*; Sd = *Perisesarma darwinensis*; Nm = *Neosarmatium meinerti*. Each experiment included six *N. meinerti* but twenty of each of the other species (half male and half female; half small and half large). See the text for further details

	Electivity on common species					
	Experiment 1: dry season			Experiment 2: wet season		
Crab species	Ps	Pd	Nm	Ps	Pd	Nm
	Am	Am	Am	Am	Am	Am
	Ca	Ca	Ca	Ca	Ca	Ca
Leaf species	Rs	Rs	Rs	Rs	Rs	Rs
	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
	Senesc.	Senesc.	Senesc.	Senesc.	Senesc.	Senesc.
Leaf condition	Decay	Decay	Decay	Decay	Decay	Decay
				Am	Am	Am
				Ca	Ca	Ca
Propagule species				Rs	Rs	Rs

Experiment 1. Electivity of leaves from three mangrove species during dry season conditions. All crab species were offered a choice of nine types of leaves, comprising all combinations of the three species (*C. australis*, *A. marina* and *R. stylosa*) and three conditions (fresh, senescent, and decayed).

Experiment 2. Electivity of leaves and propagules from three mangrove species during wet season conditions. Experiment 1 was repeated but with pieces of the propagules of all three mangrove species also offered.

Processing measurements and calculations. Consumption was measured in two ways, by weight change and by area removed, and the results of these two methods compared. The material offered had to be weighed wet but the material remaining could be weighed wet or dry. As dry weights were likely to be less variable, the material remaining was dried at 60°C for two days and then weighed. To calculate loss, the initial wet weights were converted to dry weights. This was done by taking wet and dry weights of twenty samples of the leaves and propagules of each species. These samples were then dried at 60°C for two days and remeasured. Regression equations predicting dry weight from wet were then derived and used (all $R2 > 0.8$).

After the experiments, the area processed was calculated by overlaying a clear plastic grid on top of each litter item, counting the total number of 5 × 5 mm squares that each leaf disc originally filled and the number of squares consumed. The percent of area processed was converted into dry weight processed by multiplying percent area by the converted initial leaf dry weights.

The weight loss in control treatments (treatments with no crabs) was subtracted from the weight loss of leaves and propagules in treatments with crabs, to correct for weight loss of propagules and leaves due to leaching of DOM and fungal and microbial activity.

Statistical analyses. As the crabs were presented with an array of choices simultaneously in each experiment, the amounts of the different items consumed may not have been independent (e.g. greater consumption of one item is likely to result in reduced consumption of others). Because of this, repeated measures analysis of variance (ANOVA) was used for analysing all data in this study. Assumptions for ANOVA were tested with Cochran's homogeneity of variances test and data were transformed when appropriate. Mauchley's Sphericity test was used to check the assumptions required for repeated measures ANOVA and, when these could not be met, the Greenhouse Geisser correction was applied (Winer *et al.* 1991).

Several analyses were done: each included as many factors as possible (chosen to test hypotheses a priori) so as to limit the total number required. Data for *P. semperi* and *P. darwinensis* in Experiments 1 and 2 could be analysed together as the same numbers, sizes and sexes of crabs were used and all were offered similar choices. Analyses including crab size were based on absolute mean consumption rates for the two groups (and was not weight specific). Data for *N. meinerti* in Experiments 1 and 2 had to be analysed separately as the choices offered to the crabs differed. For all experiments, two sets of analyses were done. One set compared the seasons but used only the data for leaves (as propagules were not offered in the dry season). The second set considered only the wet season but included the data for propagules.

Factors in analyses varied, depending upon the design, but included season (wet, dry), crab species (*P. semperi, P. darwinensis*), crab sex (male, female), size class of crab (small, large), species of material (*A. marina, R. stylosa, C. australis*) and type/condition of material (fresh, senescent or decayed leaf; propagule). Some of the resulting analyses were complex (i.e. Table 3). Inspection of every higher order interaction in such analyses is likely to be tedious and potentially unrewarding. Following Mead (1988), our interpretation of such analyses focused on sources of variation which were significant and which, judged by the magnitude of the relevant mean square, accounted for a substantial proportion of the variance.

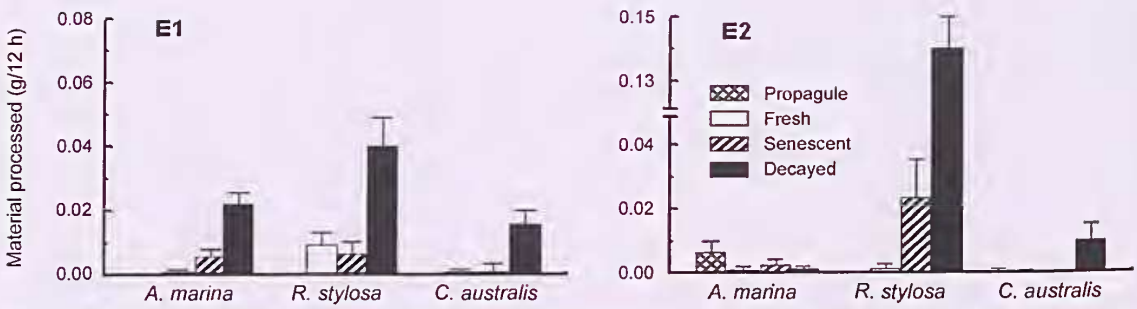

Fig. 1. Consumption of material (g dry weight per 12 hours) from three mangrove species – *A. marina*, *R. stylosa* and *C. australis* – by *N. meinerti* in electivity experiments (mean + SE). Note change in y-axis scale on graph for Experiment 2 (E2). For further details see Table 1.

RESULTS

Comparison of analyses based on leaf weight processed and leaf area processed. Overall, results from analyses based on weight and area were usually very similar, although analyses of area consumed gave more significant effects in the statistical analyses. This was probably due to greater variability in estimates based on weight (than on area). With measurements based on weight, the initial observations, as they were of wet weights, were likely to be more variable and the conversion of these to dry weight, using the regression equations, probably introduced additional errors. As there were relatively few such differences, and they did not affect the overall interpretation of the experiments, results in the rest of the study are presented here from weights estimated from area consumed.

Neosarmatium meinerti. Processing of leaves, in general, depended upon the season, species and type/condition of material when crabs were offered (see Table 2 for specific factors affecting processing in each experiment; Figure 1). The amount of decayed leaves processed was nearly always greater than that of senescent or fresh leaves, with the latter usually least preferred. Crabs processed more *R. stylosa* than *A. marina* or *C. australis*, particularly in the wet season when processing of some items increased markedly (Figure 1: E1 v E2).

When propagules were offered with leaves (Experiments 2), processing still depended upon the species and type/condition of material (Table 2). Of the propagules, only *A. marina* were processed and only in moderate amounts; senescent and decayed leaves were processed in greater quantities.

Perisesarma semperi. Patterns in processing of leaves by *P. semperi* were complex, with numerous interactions between the different factors in the analysis (Table 3). Judged by the magnitude of the mean squares, the major effects were of the species and type/condition of material, and their interaction, and the interaction between crab size and season. The overall pattern of results was very similar to that seen with *N. meinerti* – greater processing of decayed material than the other types, and of *R. stylosa* than of the other species – although there was no increased processing in the wet season (Fig. 2: E1 v E2). An interaction between season and crab size (Table 3) occurred because large crabs processed more leaf material in the dry season than small crabs, but there was no difference between sizes in the wet (means = 0.015 g/12 hours for large crabs in the dry season, and 0.007 g/12 hours for small; 0.019 g/12 hours for large crabs in the wet season, and 0.020 g/12 hours for small). Interactions between size, season and other factors (Table 3), however, indicate that the strength of this pattern depends on the crab and mangrove species, and the condition of the material. Interactions with crab sex were also significant, although of less importance (Table 3).

When propagules were offered, the results were again similar to those for *N. meinerti*: a moderate amount of *A. marina* propagules was processed while other species

Table 2. Results of repeated measures analyses of variance of amount of material processed (weights based on areas) by *Neosarmatium meinerti* in all experiments using all common species (E1, E2). The table gives the df, MS and significance (* = $P < 0.05$; *** = $P < 0.001$) for two analyses: the first used data for leaves only but included two seasons (wet and dry); the second used data for leaves and propagules but only for the wet season. Only the main effects and significant interactions are shown. Effects with fractional df have the Geisser-Greenhouse correction applied. See Table 1 for further information on the design of the experiments.

	Electivity for common species			
	Leaves only: E1, E2		Leaves, propagules: E2	
Factor	df	MS	df	MS
Season	1, 9	0.032		
Species (Sp) of material	1.25, 18	0.076	2, 10	0.730*
Type/Condition of material	2, 18	0.075*	3, 15	0.901***
Season × Sp	2, 18	0.013		
Season × Type	2, 18	0.102*		
Sp × Type	4, 36	0.025	6, 30	0.230
Season × Sp × Type	4, 36	0.066*		

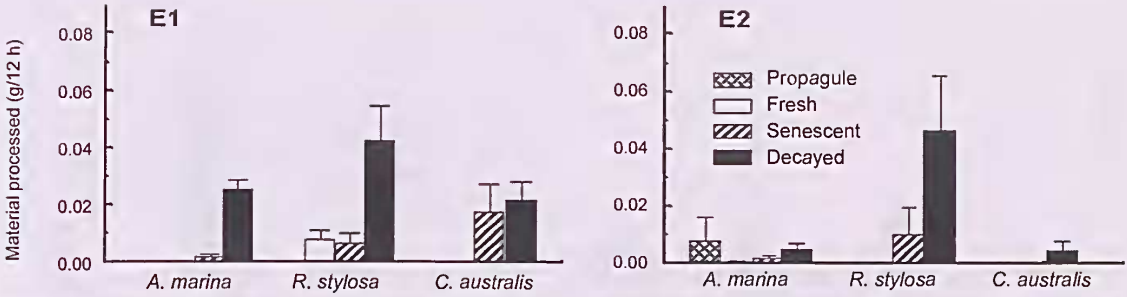

Fig. 2. Consumption of material (g dry weight per 12 hours) from three mangrove species – *A. marina*, R. *stylosa* and *C. australis* – by *P. semperi* in electivity experiments (mean + SE).

were ignored (Fig. 2: E2). In Experiment 2, when materials including propagules were offered, there was a substantial effect of crab size (Table 3), but the interactions indicated that the pattern was only observed for *P. darwinensis* (see below).

Perisesarma darwinensis. Results for the consumption of commonly available species by *P. darwinensis* were broadly similar to those of the other two crab species (Table 3; Fig. 3) – the major effects were of the species and type/condition of material and their interaction – but there were differences in detail. While *P. darwinensis* still tended to consume greater amounts of decayed leaves, greater amounts of senescent and even fresh, leaves were taken by this species (Fig. 3). In fact, in the dry season, roughly equal amounts of all three types of *C. australis* leaves were taken; and there was similar consumption of *R. stylosa* decayed, and *A. marina* senescent and decayed, leaves (Fig. 3: E1). As with *N. meinerti*, there was a markedly increased consumption of *R. stylosa* material in the wet season (Fig. 3: E2). In contrast to the dry season, fresh and senescent *C. australis* leaves were not taken at this time.

In Experiment 2, as noted above, when commonly available materials, including propagules, were offered there was a substantial effect of crab size (Table 3),

Table 3. Results of repeated measures analyses of variance of amount of material processed (weights based on areas) by *Perisesarma semperi* and *P. darwinensis* in Experiments 1 and 2. See Table 1 for the design of the experiments and Table 2 for the format of the table.

	Leaves only: E1, E2		Leaves, propagules: E2	
Source	**df**	**MS**	**df**	**MS**
Season	1, 60	0.018		
Crab species	1, 60	0.055 *	1, 28	0.198 *
Sex of crab	1, 60	0.031	1, 28	0.036
Size class of crab	1, 60	0.009	1, 28	0.578 **
Species (Sp) of material	1.31, 120	0.337 ***	1.6, 56	1.416 ***
Type/Condition of material	1.46, 120	0.826 ***	2.25, 84	1.871 **
Season × Size	1, 60	0.152 ***		
Sex × Sp	1.31, 120	0.032 *	1.6, 56	0.055
Sex × Type	1.46, 120	0.049 **	2.25, 84	0.049
Sp × Type	4, 240	0.140 **	6, 168	1.004 ***
Season × Size × Sp	1.31, 120	0.054 **		
Crab × Sex × Type	1.46, 120	0.036 *	2.25, 84	0.148 *
Season × Size × Type	1.46, 120	0.072 **		
Crab × Size × Type	1.46, 120	0.005	2.25, 84	0.172 *
Sex × Size × Type	1.46, 120	0.024	2.25, 84	0.192 *
Crab × Sp × Type	4, 240	0.045 ***	6, 168	0.071
Sex × Sp × Type	4, 240	0.023 *	6, 168	0.025
Season × Crab × Size × Type	1.46, 120	0.031 *		
Season × Sex × Size × Type	1.46, 120	0.021 *		
Crab × Sex × Sp × Type	4, 240	0.047 ***	6, 168	0.063
Season × Size × Sp × Type	4, 240	0.053 ***		
Sex × Size × Sp × Type	4, 240	0.002	6, 168	0.166 **
Season × Crab × Sex × Size × Sp	1.31, 120	0.046 **		
Season × Crab × Sex × Size × Type	1.46, 120	0.038 *		
Season × Sex × Size × Sp × Type	4, 240	0.035 **		
Season × Crab × Sex × Size × Sp × Type	4, 240	0.043 **		

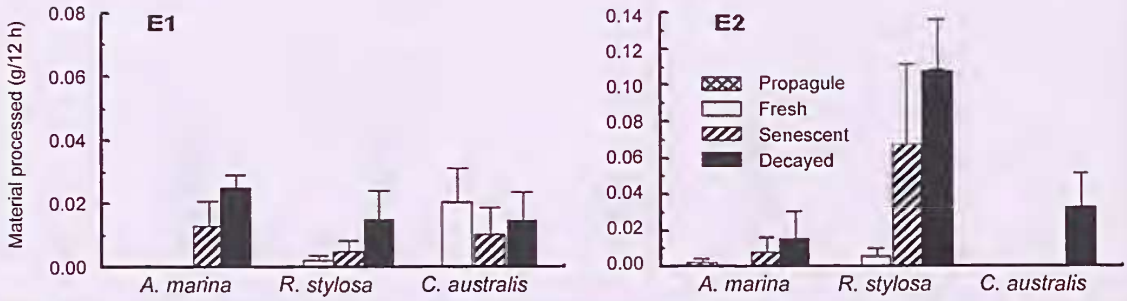

Fig. 3. Consumption of material (g dry weight per 12 hours) from three mangrove species – *A. marina*, *R. stylosa* and *C. australis* – by *P. darwinensis* in electivity experiments (mean + SE). Note change in y-axis scale on graph for Experiment 2 (E2). For further details see Table 1.

with large crabs processing more material than smaller crabs (means = 0.013 g/12 hours, and 0.002 g/12 hours, respectively).

DISCUSSION

A common trend in the present study was selectivity for older material. When offered common species, *N.meinerti* and *P. semperi* consumed more decayed *R. stylosa* leaves than any of the other options (Table 4). *Perisesarma darwinensis* displayed a similar pattern in the wet season, although not in the dry. The second and third most consumed materials were also usually decayed or senescent leaves, although *P. darwinensis* electivity again differed in the dry season. Other studies have documented similar electivity for older material. In northeastern Australia, Camilleri (1989) found *Sesarma erythodactyla* preferred aged leaves to freshly fallen leaves and Micheli (1993) found *Sesarma messa* preferred decayed leaves over senescent leaves. In Kenya, *Neosarmatium smithii* (= *Sesarma smithii*) preferred old or decaying leaves over young leaves (Micheli 1991; Table 5). Ashton (2002), however, found two Malaysian species, *Sesarma eumolpe* and *Sesarma onychophorum*, preferred fresh to senescent *Avicennia officinalis* leaves.

Studies have shown that decaying leaves have a lower concentration of tannins than fresh leaves, so may be more easily digested and preferred for this reason (Giddins *et al.* 1986; Neilson *et al.*1986). A study by Micheli (1993), testing for the effects of tannin, found no significant correlation on the feeding preferences of *N. smithii* and *S. messa*. These tests were, however, done with senescent, rather than decaying, leaves (including *R. stylosa*, *C. australis* and *A. marina*) and Robertson (1988) found that the tannin content of these leaves decreased rapidly over the first 14 days of decomposition. Thus, the range of tannin concentrations in senescent leaves might not be large enough to affect electivity.

Studies of sesarmid electivity for material from different mangrove species, in contrast to material of different ages, have given more variable results. Micheli (1993) found that *N. smithii* preferred *R. stylosa* to *A. marina*, *Bruguiera exaristata* and *C. australis*; results similar to *P. semperi* here. Camilleri (1989) found *S. erythrodactyla* selected *R. stylosa* least, after *A. marina* and *B. exaristata*. Ashton (2002), with *S. eumolpe* and *S. onychophorum*, found a preference for *A. officinalis* but only in fresh leaves. With *S. messa*, however, Micheli (1993) found no significant preference among the species tested and Dahdouh-Guebas *et al.* (1997), studying *N. meinerti* in Kenya, also found no preference, although only fresh material was offered. Olafsson *et al.* (2002), however, also tested *N. meinerti* from Kenya and obtained results similar to Camilleri (1989) for *S. erythrodactyla*. Greater electivity of *A. marina*, as also exhibited on occasion by *P. darwinensis* in the present study, can be explained by the particularly low tannin and high nitrogen levels characteristic of this species (Robertson 1988; Camilleri 1989; Michelli 1993). Leaf nitrogen, in particular, is usually a reliable predictor of herbivore preference in both laboratory and field situations (Perez-Harguindeguy *et al.* 2003). Mature leaves from *A. marina* in Darwin Harbour have been shown to have significantly higher nitrogen concentrations than *R. stylosa* and *C. australis* (Coupland 2002). *Rhizophora stylosa* leaves, in contrast, have lower nitrogen concentrations and higher percentage of tannin, than *A. marina* (Robertson 1988; Coupland 2002) and electivity for this species is more difficult to explain.

Table 4. Summary of electivity exhibited by the three species of sesarmids. Am = *A. marina*; Ca = *C. australis*; Rs = *R. stylosa*; f = fresh leaf; s = senescent leaf; d = decayed leaf; p = propagule.

	Species	1st choice	2nd choice	3rd choice
Dry Season	*N. meinerti*	d–Rs	d–Am	d–Ca
	P. semperi	d–Rs	d–Am	d–Ca, s–Ca
	P. darwinensis	d–Am	f–Ca	several
Wet Season	*N. meinerti*	d–Rs	s–Rs	d–Ca, p–Am
	P. semperi	d–Rs	s–Rs, p–Am	
	P. darwinensis	d–Rs	s–Rs	d–Ca

Table 5. Summary of electivity/preferences for leaves of different species and conditions exhibited by sesarmid crabs in other studies. Am = *A. marina*; Ca = *C. australis*; Ct = *C. tagal*; Bg = *Bruguiera gymnorhiza*; Be = B. *exaristata*; Rm = *R. mucronata*; Rs = *R. stylosa*; Sa = *Sonneratia alba*; f = fresh leaf; s = senescent leaf; d = decayed leaf; Nm = *N. meinerti*; Ns = *N. smithi*; Sm = *S. messa*; Se = *S. erythrodactyla*; Ce = *C. carnifex*. Note: all species/conditions that were used in the trials are included below. *No pattern in electivity/preference.

Study	Field/lab	Species	1st choice	2nd choice	3rd choice	4th choice	5th choice
Steinke *et al.* 1993	Field	Nm	s–Bg	s–Am	f–Bg	f-Am	
Giddins *et al.* 1986	Lab	Ns	d–Ct	s–Ct	f–Ct		
Micheli 1993	Lab	Sm	s–Am, s-Rs, s-Ct, s-Be*				
	Lab	Nm	s–Rs	s–Am, s-Ct, s-Be			
	Lab	Sm	d–Am, d-Rs, d-Ct, d-Be	s–Am, s-Rs, s-Ct, s-Be			
	Field	Nm/ Sm	s-Ct	s-Rs, s-Re, s-Am			
Camilleri 1989	Lab	Se	d–Am	d–Bg	d-Rs	s-Am	s-Bg; s-Rs
	Lab	Se	f-Am, d-Am	s-Am			
	Lab	Se	d-Rs	s-Rs			
Micheli *et al.* 1991	Lab	Ce	s–Bg	s–Sa	s-Rm	s-Ct	s-Am
	Lab	Nm	s-Bg, s-Sa, s-Rm, s-Ct, s-Am*				

Camilleri (1989) found that crabs preferred thicker *R. stylosa* leaves, so other leaf attributes may be influential (such as moisture, fibre content and other chemical constituents). Kennish and Williams (1997), in a study of the tropical rocky shore crab *Grapsus albolineatus*, concluded that algal morphology, through effects on feeding efficiency, was more important than nutritional value or digestibility. And Chavanich and Harris (2002) suggested that several factors, including morphology and nutritional value, probably influenced the feeding preferences of the subtidal gastropod *Lacuna vincta*. Previous experience by the crabs may also be important (Perez-Harguindeguy *et al.* 2003) and explain some of the varying results for *N. meinerti,* which has shown no particular pattern in electivity (Micheli *et al.* 1991; Dahdouh-Guebas *et al.* 1997) and electivity for (Olafsson *et al.* 2002) and against (Steinke *et al.* 1993; this study) *A. marina*. It does not, however, appear to hold true for crabs in the present study, since they did not usually, when offered a range of common species, select species from the assemblage in which they were most abundant (in contrast to the results of Ashton (2002)).

Crab electivity within a restricted range of material, representative of probable encounter rates, may differ from electivity when all mangrove leaves and conditions are offered in equal proportions. In a recent study on the gypsy moth (*Lymatria dispar*) for example, Raffa *et al.* (2002) found that results could be affected by the combination and arrangement of choices, and also by total consumption. Perez-Harguindeguy *et al.* (2003) concluded that laboratory preference experiments can predict relationships in the field, but ecological factors such as variations in accessibility and specialised plant-herbivore relationships can cause differences. However, according to the model they developed, predictions are likely to be reliable for generalist herbivores and plants of high accessibility, both conditions which apply here to various extents. Together, these points suggest that strong, general trends, such as the electivity for older material, are likely to apply in the field. In contrast, more precise distinctions between species and ages of material may be situation-specific. Further study of weight-specific consumption rates, and experiments offering different proportions of materials would shed light on the different patterns observed here.

Given the importance of sesarmid crabs as propagule predators (Smith 1987; McGuinness 1997; Lee 1998), the limited consumption of propagules in the present study, particularly by *N. meinerti*, is surprising. The *Perisesarma* species may be too small to deal effectively with propagules but *N. meinerti* is known to consume them in the field (McGuinness 1997; Dahdouh-Guebas *et al.* 1997). On the basis of these results, however, leaf material is preferred, when it is available. Further, studies have found from 75% (Steinke *et al.* 1993) to 90% (Dahdouh-Guebas *et al.* 1997) of the material in *N. meinerti* stomachs to be leaf material, although Skov and Hartnoll (2002) reported only 10% of crabs feeding on leaves compared to 76% feeding on mud. In part, the difference may result from the differing digestibility of material: this would be consistent with the results of Bouillon *et al.* (2002), whose stable isotope studies indicated that sesarmid crabs fed on a wider range of material than just mangrove leaves.

Effects of size and sex of crab were inconsistent, although in accordance with previous results. Emmerson and McGwynne (1992) reported a correlation between size and consumption for *N. meinerti* in southern Africa. Furthermore, Olafsson *et al.* (2002) found greater consumption by female crabs, and they suggested this could be due to either the difference in size between the sexes, with females being smaller and having a higher potential for energy loss, or to reproductive demands. The latter explanation is perhaps more likely as size was controlled in experiments here. Further, Micheli (1993) observed more ovigerous crabs during the late dry season and this might partially explain greater consumption at this time.

In conclusion, this study confirms the general pattern in electivity of sesarmids for older material observed in

most other studies but also demonstrates that the range, and types, of material offered can affect electivity. The amount consumed depends upon the size of the crab, and is likely to depend upon its sex and reproductive state. Furthermore, the results suggest that sesarmid crabs included in this study have a greater role in nutrient cycling than in forest structuring because of their selectivity of leaves over propagules. Hence, sesarmids in northern Australia appear to have a distinct overall ecological role than in other regions such as shown in some studies in new world mangrove forests (Smith *et al.* 1991). Future studies should attempt to confirm the findings here by; investigating weight specific consumption rates, determining whether 'feeding preferences' differ from 'feeding electivity' (Underwood *et al.* 2004), and ultimately determining the reasons underlying the high variability in sesarmid feeding selectivity for leaves of different mangrove species, observed in the majority of studies conducted thus far.

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